Oviposition Behavior and Host Feeding of *Asaphes lucens*[1] an Aphid Hyperparasitoid[2]

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Abstract: The behavioral study of the hyperparasitoid *Asaphes lucens* was greatly facilitated by the development of a technique which partially exposed its host *Aphidius smithi* within the mummy. This exposure allowed direct observation of ovipositional exploration, host venomization, feeding tube formation, and actual egg deposition.

After antennal investigation of the mummy surface, the *A. lucens* female spent an average of 4.3 min drilling through the mummy to reach the host. The hyperparasitoid then used her ovipositor to explore the host, spending an average of 7.5 min in this activity. Prior to the first oviposition, *A. lucens* always constructed a feeding tube from host body to mummy surface, and then fed for an average of 5 min. Once feeding was completed the tube was always broken by a reinsertion of the ovipositor.

Successful biological control programs demand not only a thorough understanding of those insect populations directly involved, but require a study of peripheral factors as well. For this reason we have investigated the ovipositional and host-feeding behavior of the hyperparasitoid *Asaphes lucens* (Provancher) as it attacks the primary parasite *Aphidius smithi* Sharma and Subba Rao. A detailed knowledge of the biology and behavior of the hyperparasitoid is important if the entire complex of host-primary parasite-secondary parasite is to be understood.

Extensive reviews of the biology, ecology and impact of aphid parasitoids in general were made by Clausen (1940), DeBach (1965) and Hagen and van den Bosch (1968), but very little work has been directed specifically toward the aphid hyperparasitoid *A. lucens*. Griswald (1929) discussed the immature stages of *A. lucens* and certain aspects of the behavioral pattern of this species have been investigated and recorded by Spencer (1926) who observed that *A. lucens* examines the aphid mummy prior to attacking the primary parasite it contains. Sekhar (1958) examined the drilling process which gives the parasitoid access to its host, thus allowing for oviposition, but host feeding was not observed in

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A. lucens. However, Sullivan (1972) did report this behavior in another species, *A. californicus*.

The present investigation was undertaken to examine in detail the ovipositional behavior of *A. lucens*, to determine whether or not this species follows the usual pattern of other nonaphid attacking Pteromalids, and whether it does indeed host feed. The development of a technique whereby the interior of the aphid mummy could be viewed during the entire ovipositional act greatly facilitated this study.

MATERIALS AND METHODS

The pea aphid *Acyrthosiphon pisum* (Harris) served as host in this study, and was reared on broad bean, *Vicia fava* Linnaeus (Windsor variety). *A. smithi* Sharma and Subba Rao, the primary parasite, and *A. lucens* (Provancher), the hyperparasitoid, were reared with the plants and aphids in a temperature cabinet (percival Environator, Model E–54U).

To observe the process of oviposition or feeding tube formation, a parasitized aphid or "mummy" was affixed, ventral side down, to a 3 cm square of paper in a drop of Elmer's Glue-All (Borden Chemical Co.). Using a micro-scalpel and a microprobe, one lateral surface and half the dorsal surface of the mummy were cut away, thus partially exposing the primary parasitoid, and still allowing sufficient dorsal surface for the hyperparasitoid to take the ovipositional stance and begin drilling. In this way, the action of the ovipositor within the mummy and feeding tube formation could be observed.

RESULTS AND DISCUSSION

Ovipositional behavior. The process of oviposition by *A. lucens* was both preceded and followed by a fairly predictable behavior pattern. The female approached the aphid mummy containing the primary parasitoid and began an intensive examination, consisting first of rapidly walking around, and sometimes over, the mummy. This initial exploration usually lasted only a few seconds and was then followed by a more lengthy period of antennal tapping, extending from 1 to 30 seconds. The parasitoid bent her antennae downward and appeared to use them to examine most of the mummy surface. At times her abdomen would be stretched out just above the mummy, in an almost "listening" posture. Occasionally, the examination proceeded no further than this. For some reason, the female would simply leave the mummy, perhaps to return and repeat the process, or perhaps to find another more suitable host.

Should the investigation continue, the female was seen to squat slightly and lightly tap the mummy with the tip of her abdomen, apparently searching for the right location for the insertion of her ovipositor. When this spot was found,

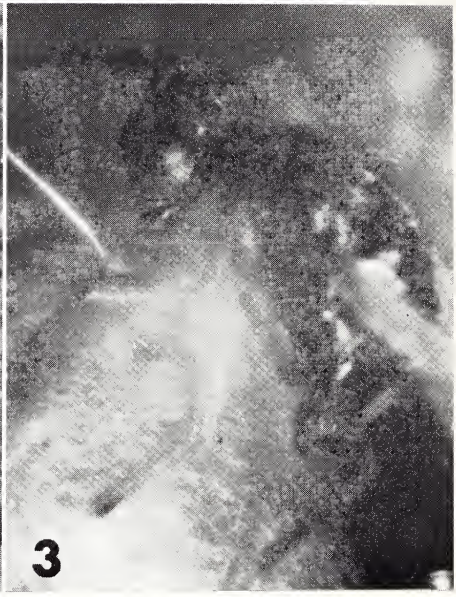

Fig. 1. —Two *lucens* hyperparasitoids attacking a mummy containing the primary parasitoid *A. smithi*. The female in the lower right is examining the mummy with her antennae, while another female drills with her ovipositor.

Fig. 2. —Partially opened mummy showing transparent feeding tube (a) extending from *A. smithi* larva to the surface of the mummy. (Retouched photograph).

Fig. 3. *A. lucens* female feeding at drill hole.

usually after an average of 1.5 min, the preliminary phase of oviposition ended and the drilling phase began (Fig. 1).

While drilling, *A. lucens* assumed a characteristic stance. The body was in a squatting, partly vertical position, head and antennae were bent downward, the legs were apart, and the feet were firmly anchored on the mummy surface, giving leverage to the ovipositor. Drilling was accomplished by a circular rotation of the ovipositor, and by an up and down movement of its valves against each other. Once drilling was completed, the ovipositor was thrust completely into the mummy, so that at times the female's abdomen touched the mummy surface.

The amount of time necessary for the female to successfully drill through the aphid mummy varied greatly, depending on the density of the cocoon spun within by *A. smithi*. In one instance, 24 minutes were needed, while several females completed the task in 1 minute or less. The average drilling time was 4.3 minutes.

None of the earlier investigators of *A. lucens* (Spencer 1926; Griswald 1929; Sekhar 1958) have recorded what takes place inside the mummy as the female explores with her ovipositor, and finally venomizes and oviposits on the host. The use of a partially opened mummy allowed direct observation of the ovipositor within the mummy.

The female used her ovipositor to probe and stroke the host surface. She reached the most distal parts of the host at least with the tip of her quite flexible ovipositor. The average time spent exploring the host in this manner was 7.5 minutes for each insertion of the ovipositor. If it is customary for the female to spend this amount of time in a tactile study of her host, then it would indicate that the organ of exploration must be equipped with sensory structures of some sort. Several parasitoids have been studied for the presence of just sensory structures and the electron microscope has revealed their presence on the tip and sheath of the ovipositor, as well as the occurrence of sensory pits on the 1st valvulae (Gutierrez 1970; Weseloh 1971, 1972). An EM study of the ovipositor of *A. lucens* may reveal similar sensilla.

Very little work has been done on the venom used by hyperparasitoids. That *A. lucens* does venomize her host has been observed in the course of these investigations. The *A. smithi* larva contracted and jerked away when *A. lucens* explored the host surface; when the ovipositor was inserted into *A. smithi* its activity ceased within an average of 2 minutes. Although Clausen (1940) recorded instances of a 10 minute to an 8 hour lag until the venom of other parasitic Hymenoptera took effect, the venom of *A. lucens* was fast acting. While Beard (1963) insisted that paralyzing venom is not a preserving fluid, several paralyzed *A. smithi* larvae have been found to remain soft and moist up to 14 days, although they had turned brown.

The complete withdrawal of the ovipositor in the species was always preceded by a characteristic movement of the antennae. During the entire process of preliminary investigation, drilling, and host examination, the antennae were bent downward. When the ovipositor was to be finally removed from the mummy, the antennae were raised to a horizontal position and fluttered slightly. This signaled a complete withdrawal of the ovipositor as opposed to the partial withdrawals noted above.

The actual passage of the egg from parasite to host has been observed in this study. Rather than appearing compressed within the ovipositor (Fulton 1933), the egg of *A. lucens* glides along the valves, which appear separated, and serve as rails or guides. There seemed to be no distortion of the egg during oviposition, nor any sudden increase in size immediately after. The egg was usually, but not always, deposited on the inner, ventral curve of the larval or pupal body of the host.

It was not unusual for *A. lucens* to withdraw her ovipositor, sometimes even leave the mummy and return, and then reinsert the ovipositor either into the same hole or drill a new hole. This behavior represents multiple attacks on a single host by the same parasitoid and these data are at variance with the findings of Sekhar (1958). Not only does *A. lucens* sometimes attack the same mummy more than once, as was reported by Sullivan (1972), but an unpredicttable number of eggs are laid as a result of these attacks.

Host feeding. The present observations indicate that not only does *A. lucens* feed at the drill hole, but that it also constructs a semi-transparent feeding tube extending from the surface of the host to the surface of the mummy. After feeding, the ovipositor is always reinserted into the same opening, the feeding tube broken, and the act of oviposition begun. It should be noted, though, that host feeding activity usually accompanies only the first oviposition of a female. Later egg deposition does not include feeding tube construction and host feeding. Using partially opened mummies, the sequence of host feeding behavior was as follows:

1. After drilling through the mummy surface, *A. lucens* paralyzed and examined the host larva with her ovipositor. Several times during this exploratory process, the parasitoid partially withdrew her ovipositor; it was after the last of these partial withdrawals that feeding tube construction was begun.

2. With extreme slowness and deliberation, the ovipositor, still in the original drill hole, was lowered until its tip pierced the body of the primary parasite. Just as slowly and carefully the ovipositor was then completely withdrawn, being continuously twisted until it was free of the mummy. This pains-taking withdrawal usually took from 5 to 19 min, and left behind a feeding tube extending from host to mummy (Fig. 2).

3. Once the ovipositor had been completely withdrawn, *A. lucens* turned and began to feed at the puncture. The average feeding time was 5.3 minutes (Fig. 3).

4. Feeding was always followed by the reinsertion of the ovipositor into the drill hole, and the breaking of the fragile tube with a rapid, thrusting motion. In several instances a marked decrease in the volume of the host could be observed after feeding by *A. lucens*.

5. Normally, eggs were then deposited on the host, the ovipositor withdrawn, and the process terminated.

6. Occasionally however, the ovipositor was first withdrawn and then reinserted into the puncture, and then one or more eggs were deposited on the surface of the *A. smithi*.

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